

BIOLOGY AND BEHAVIOR OF BREEDING PIPING PLOVERS

WINIFRED E. CAIRNS

The Piping Plover (*Charadrius melodus*) is an endemic species of central and eastern North America which breeds discontinuously throughout its range in suitable sand beach habitat. Apart from early accounts such as those by Bent (1929) and Wilcox (1939), a single study by Wilcox (1959) provides most of the breeding information known for the species. An assessment of the numerical status of the population in eastern North America is contained in Cairns and McLaren (1980). The present study was undertaken to obtain baseline information on the Piping Plover in Nova Scotia. Emphasis was placed on detailing the biology and behavior associated with the nesting cycle, and on examining the relationship between nesting success and the multiple use of beaches.

STUDY AREA AND METHODS

The major study area was at Cadden Beach, southern Nova Scotia (43°50'N, 64°50'W), and consisted of a sandspit 1.4 km long and 75-200 m wide. This broad, relatively flat expanse of unconsolidated sand was strewn with gravel, clods of peat, driftwood, and other debris. Across most of the spit vegetation was extremely scanty, consisting of seabeach sandwort (*Arenaria peploides*) and to a lesser extent marram grass (*Ammophila breviligulata*). Studies at this site were carried on from 1 May-15 August 1975 and from 22 April-10 August 1976. Additional data were obtained from May-August 1976 during visits to eight other beaches in Nova Scotia where *C. melodus* breeds, and from observations in 1977, 1978, and 1979 at numerous breeding sites throughout Atlantic Canada.

Adult Piping Plovers were captured on their nests by a drop trap or a circular walk-in trap. Adults were sexed by a combination of behavior and plumage characteristics: in general the male of a pair had the darker neck band. Chicks were banded as they hatched or when first encountered. I banded 14 adults and 53 chicks in 1975, and 11 adults and 91 chicks in 1976. Nineteen adults in 1975 and four in 1976 were color marked. After hatching, chicks were recaptured and weighed as often as possible.

In 1976 I estimated 27-29 pairs of Piping Plovers were present and 96 chicks were hatched on Cadden Beach (based on the number of chicks encountered from known nests compared with numbers encountered from nests not found by me, as well as other circumstantial evidence). Approximately 10 non-breeding birds also occupied the beach each year.

RESULTS AND DISCUSSION

Fidelity to nesting area.—In Nova Scotia most Piping Plovers arrive from mid- to late April and initially feed in areas unclaimed as territories, where aggressive interactions are numerous. Such early-season flocking places birds of both sexes in close proximity, and in high density beaches may speed up the development of behavior associated with territorial es-

tablishment and courtship. This is suggested by later hatching dates for beaches where only one or two pairs occur.

At least some birds returned to their territories a second year. Two females caught on Cadden Beach nests in 1976 had occupied the same territories in 1975. Both nested within 20 m of their nest-sites of the previous year. A male occupied a 1976 nesting territory that was about 1 km from his 1975 birthplace. Five other adults already banded when observed on Cadden Beach in 1976 had probably been banded there in 1975 by me.

The tendency for adults to return to a former breeding area (and sometimes nesting territory as well) has been reported for Piping Plovers (Wilcox 1959) as well as for a number of other plover species including Ringed Plover (*C. hiaticula*) (Laven 1940, Bub 1962), Killdeer (*C. vociferus*) (Lenington and Mace 1975), Kentish Plover (*C. a. alexandrinus*) (Rittinghaus 1956), Mountain Plover (*C. montanus*) (Graul 1973b) and Northern Lapwing (*Vanellus vanellus*) (Spencer 1953). Few first year birds return to breed in the area of hatching among *Charadrius* plovers, as suggested by ca. 5% return rates for Ringed, Piping and Kentish plovers (Lenington and Mace 1975).

Spacing and territory size.—Of the approximately 0.2 km² of raised sandspit on Cadden Beach, about 0.12 km² was prime Piping Plover nesting habitat, and was largely divided up into about 28 contiguous nesting territories, ranging from 500–8000 m² and averaging about 4000 m² in size. Feeding territories on the tidal sandflats were defended seaward from stretches of shoreline 50–100 m long. Nesting and feeding territories were usually contiguous, except in densely populated areas where some birds had to cross neighboring nesting territories to reach their feeding territories. Both types of territories were maintained throughout the season by breeding pairs. Unmated males, non-breeding pairs, and pairs that lost a clutch or brood too late to renest also maintained both kinds of territories. Distances to nearest neighboring nests on Cadden Beach averaged 51 m for the 23 nests found in 1975 and 53 m for the 27 nests in 1976 (including three known re-nests). The closest simultaneously active nests were 3 m apart.

Territory sizes among plovers vary greatly ranging from 190 m in Wilson's Plover (*C. wilsonia*) (Tomkins 1944) to 0.16 km² in Mountain Plover (Graul 1973b). Size of territory probably reflects, at least in part, the relative amounts of feeding done within the territory and in areas outside. The Red-capped Dotterel (*C. ruficapillus*) population described by Hobbs (1972) fed at a site 3 km from the breeding grounds, probably an extreme case of distance between feeding and nesting sites. Ringed Plovers (Mason 1947) and Little Ringed Plovers (*C. dubius*) (Simmons 1956) have been reported to feed mainly on neutral feeding areas, while Mountain (Graul

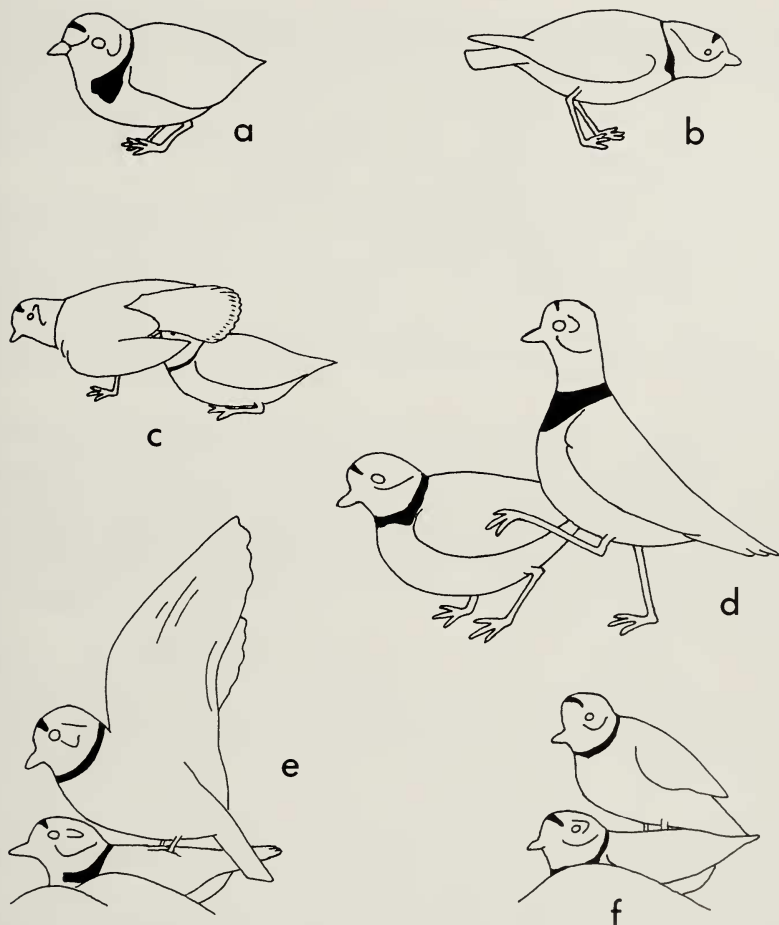


FIG. 1. Courtship postures: (a) territorial male with exaggerated neck band, (b) posture used during low gliding run, (c) female thrusting beak among feathers beneath male's tail, (d) male performing rapid high-stepping tattoo beside female, (e) mounting, and (f) copulation.

1973b) and Piping plovers do most of their feeding within their own territories.

TERRITORIAL BEHAVIOR

Establishment and maintenance.—Upon arrival males begin to establish territories; 8–10 had been set up when observations began on 22 April 1976. During territorial establishment, males spend much time on their prospective nesting territories. Thoroughly traversing the area in brief

flights and runs, they stop periodically and remain motionless except when scanning or preening (Fig. 1a). Scanning occurs at intervals and involves slowly rolling the upwardly tilted head from one side to the other. Most preening, which may last for 2 or 3 h at a time, is concentrated on the neck ring and makes it appear wider and darker. Long periods on the ground are interrupted by aerial displays and calls.

Intruders are met with horizontal threat charges, and ground or aerial chases, which aid in establishing rough territorial boundaries. These may undergo modification throughout the season as parallel run or horizontal threat displays maintain boundaries, or produce gains or losses in territory size. Agonistic activity towards neighboring birds is shown by both sexes although the male plays the greater role, particularly during territorial establishment.

Aerial displays.—Males perform elaborate flights above their territories apparently to advertise ownership to rival males and prospective females. In flight, deep, slow wing-beats and an alternate tilting of the body from side-to-side produce a fluttering flight, making the bird more conspicuous than in normal flight. Display flights, which last up to 30 min, traverse elliptical and figure eight courses from just above ground level up to ca. 35 m.

Aerial displays are usually accompanied by calls. The more common call is a continuous rapid series of high-pitched calls and sometimes is interspersed with a series of long drawn-out mournful-sounding calls.

Aerial displays and calls can arise unprovoked or can be elicited by females or other males. Sometimes two birds perform flying within a few meters of each other: these may be rival males on adjacent territories or, on occasion, mated pairs. Aerial displays and calls are sometimes given on moonlit nights but very rarely on dark nights.

Display flights and calls decline with the onset of egg-laying and incubation. One lone male that failed to attract a mate performed courtship displays regularly from the start of the 1975 field season until 19 July.

The aerial display flight of the Piping Plover resembles that described for Killdeer by Phillips (1972), and Ringed, Little Ringed, and Kentish plovers by Witherby et al. (1965).

Horizontal threat display.—Most horizontal threat displays take the form of a charge. In assuming this display posture the bird leans forward on slightly bent legs with head drawn well back into the body (Fig. 2). The neck ring becomes prominent and with increasing intensity the wings are slightly raised and the feathers of the breast, sides, and upper back are puffed. At greatest intensity the tail is fanned open and depressed, while the feathers of the back, sides, and upper breast are raised to give a ragged appearance. The low intensity display is given within a small flock by one

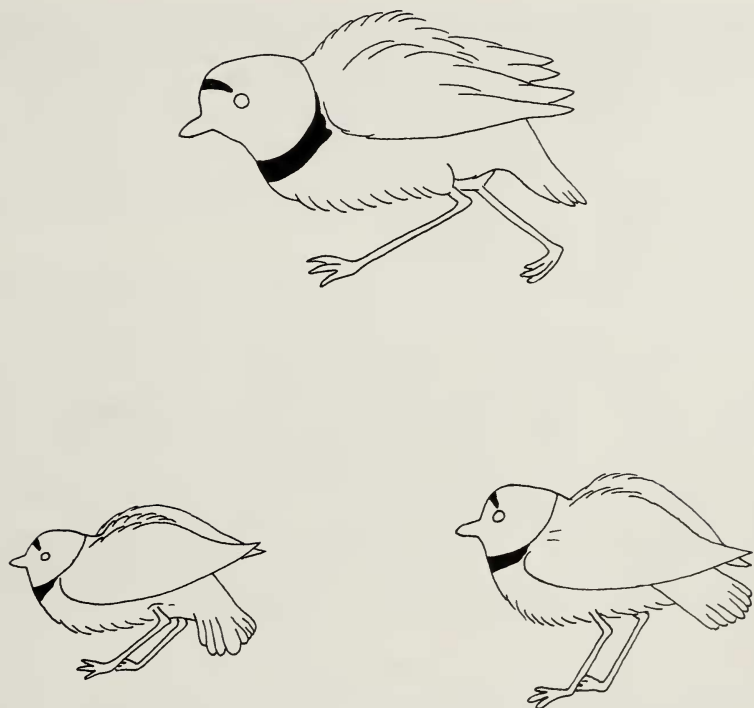


FIG. 2. Some postures used during horizontal threat display.

or more birds using low gliding runs. Then charging birds usually swerve before reaching the target bird and continuously redirect their displays toward other individuals so that actual chases and fights seldom ensue.

Encounters between two individuals more often lead to high intensity display and chases at least 30 m in length. The charging bird adopts a low intensity threat posture in a low gliding run, then increases speed and intensity. At close quarters high intensity charges occasionally terminate in brief fights. The combatants initially face each other in horizontal threat display and then jump and fly at each other, striking the bill and wings against the head, neck, and upper back regions of the opponent. Most skirmishes subsided within a few minutes as the birds gradually moved apart, often vigorously pecking the ground, or running with abrupt stops and starts. Horizontal threat displays were accompanied by a series of low rattling calls which became increasingly more rapid and took on a whirring throaty undertone as the display progressed.

Various forms of the horizontal threat display have been reported for a number of other plover species including Ringed Plover (Edwards et al.

1947, Mason 1947, Simmons 1953b), Semipalmated Plover (*C. semipalmatus*) (Sutton and Parmelee 1955), Little Ringed Plover (Simmons 1953b), Wilson's Plover (Tomkins 1944), Killdeer (Phillips 1972), Mountain Plover (Graul 1973a, 1973b) and Blacksmith Plover (*Hoplopterus armatus*) (Hall 1964). The threat display of the Piping Plover most closely resembles those of the Killdeer and Ringed Plover. These two species enlarge the neck markings and the breast feathers by fluffing them to present a rounded frontal appearance to the protagonist.

Parallel-run display.—After the establishment of territorial boundaries parallel-run displays, in which two neighbors run in parallel along a common boundary, increase in importance. Both birds adopt stiffly erect postures with heads and necks stretched upward, breast feathers puffed smoothly, and dark sides of the neck and neck ring showing sharply against the white (Fig. 3). After facing each other and head-bobbing, one bird turns at right angles and runs rapidly for a distance of 1–10 m along the disputed line. In the same manner the second bird runs past the first, often arcing into its own territory before stopping abruptly ahead of the first bird. The birds move alternately, abruptly terminating each spurt by assuming a more sharply erect posture, and bobbing the head several times.

In more intense encounters running may be interspersed with violent bouts of pecking the ground. Bouts of head-bobbing alternate with very short rapid runs, and a combination of shoulder-to-shoulder and breast-to-breast shoving may occur. Between high intensity parallel runs, close range horizontal threat charges may take place. Low intensity parallel-run displays are expressed by parallel walking or by a form of upright display in which the two opponents face each other and engage in bouts of head-bobbing alternated with neck preening or ground pecking.

The normal parallel run may cover distances of up to 100 m before the birds reverse direction and repeat the display. Encounters may continue 30 min or more, and usually conclude with the gradual withdrawal of both birds, pecking the ground as they move away from the final location of the boundary on that occasion. Vocalizations used during parallel-run displays are similar to those accompanying horizontal threat displays.

Upright threat postures have been reported in Ringed, Little Ringed and Kentish plovers (Simmons 1953b), Killdeer (Phillips 1972), Wilson's Plover (Tomkins 1944) and Mountain Plover (Graul 1973b), but only Killdeer and Mountain Plover are known to use the displays in conjunction with parallel runs. Interestingly, Ringed and Little Ringed plovers, when in upright threat display rapidly run in place, in a manner similar to the pre-mounting behavior of the Piping Plover. The general pattern among plover species of a head-up posture for defense threat and head-down posture for aggressive threat (Maclean 1972) also holds true for Piping Plovers.

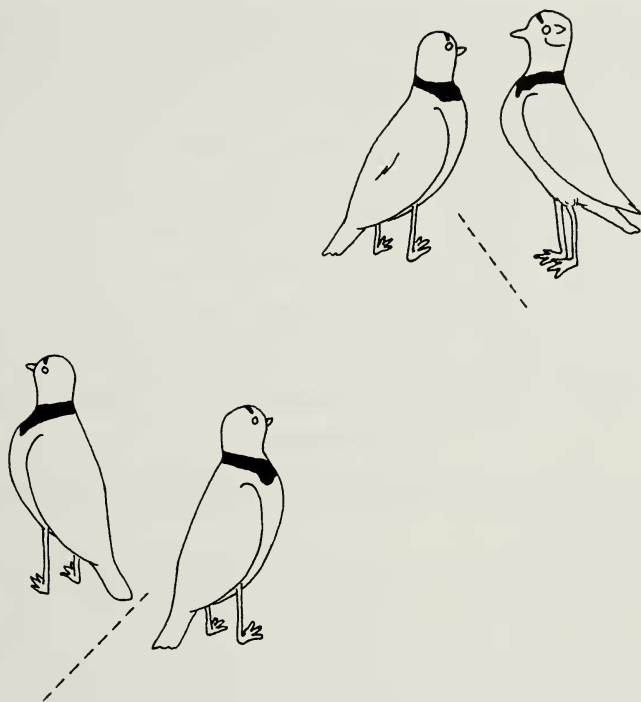


FIG. 3. Upright postures used during parallel-run displays along a common boundary.

COURTSHIP

Scraping.—A courting male on territory walks about with deliberate movements, often tossing aside sea shell fragments. Periodically he stops, squats, and, leaning far forward on his breast, pivots to the left and right, while simultaneously kicking sand backwards, producing a shallow depression or scrape in the sand. During pauses he occasionally utters one or both advertisement calls, or tosses bits of shell from the rim of the scrape into the depression beneath him. When a female is nearby the male walks or runs on bent legs, with head lowered and tail sometimes spread and elevated, squatting briefly in a number of his scrapes, of which there may be 20 or more (Fig. 1b). If the female approaches closely, the scraping male erects and spreads his tail, and increases the tempo of rotations in the scrape. Occasionally, a female following a courting male will also scrape briefly.

Tilt display.—With the female close by, the male may perform a tilt display, slowly rising to stand stiffly upright in the scrape, head, body, tail, and the partly or completely spread wings all being held in one plane, with tail elevated at an angle of about 30° (Fig. 1c). The female crouches

slightly behind the male and thrusts her beak one or more times among the feathers below the base of his tail. Alternatively, the female may approach from the side, and creeping under the male's horizontally spread tail, nestle into the sand beneath it, her body perpendicular to his. The tilt display may be repeated several times in succession at different scrapes, or the female may walk a short distance away, adopting a slightly crouched stance with legs somewhat spread, and await the approach of the male.

Mounting and copulation.—Advancing toward the female, the male slips into a low gliding crouch with head held below the horizontal and drawn well into the body. Nearing her, he gradually rises into a very erect posture with neck outstretched, neck ring conspicuously broadened and breast expanded. Simultaneously he beats a high-stepping and increasingly rapid tattoo with both feet (Fig. 1d). Upon reaching the female the male may stand by the base of her tail and continue the tattoo for a few minutes longer before flapping his wings and mounting (Fig. 1e). Copulation takes up to 1.5 min. Both birds often preen after copulation. No post-copulatory displays were seen.

Courtship in the Piping Plover basically resembles that of *Charadrius* spp. as demonstrated by Little Ringed Plover (Sluiters 1938, Simmons 1953a), Ringed Plover (Laven 1940), Snowy Plover (*C. a. nivosus*) (Boyd 1972), Mountain Plover (Graul 1973b), and Killdeer (Phillips 1972). However, none of these authors mentioned the female thrusting her bill among the feathers beneath the male's tail, as indicated above in the Piping Plover. Other differences between *C. melodus* and *Charadrius* spp. occur in the position of the wings during the tilt display; both Little Ringed (Glutz et al. 1975) and Piping plovers spread their wings on a uniform plane, while the Snowy and Mountain plovers droop the wing which is toward the female. The Killdeer apparently does not spread its wings.

The details of mounting and copulation differ somewhat with plover species. In most, males approach females in a low gliding run which somewhat resembles the posture used during low intensity horizontal threat. Before actually mounting the female, male Snowy Plovers (Boyd 1972), Red-capped Dotterels (Hobbs 1972), Killdeer (Phillips 1972), and Mountain (Graul 1973b) and Wilson's plovers (Tomkins 1944), as well as Piping Plovers adopt an upright precopulatory posture with rapid high-stepping foot movements. The Snowy (Boyd 1972) and Wilson's plovers (Tomkins 1944) are apparently the only species in which males grasp the female's neck feathers with their bills during copulation. Piping Plovers copulate anywhere within their nesting and feeding territories but Snowy Plovers (Boyd 1972), Killdeer (Phillips 1972), and Mountain Plovers (Graul 1973b) apparently only copulate at nest or scrape sites.

DISTRACTION BEHAVIOR

Piping Plovers respond to intruders (avian, human, and other mammalian) by squatting, false brooding, high-tailed running, crouch run, and injury feigning. During highest intensity distraction constant "whirring" vocalizations may be emitted. Some displaying birds have come within 2 m of me while others, after initially approaching me, have been observed to feign injury continuously while travelling up to 100 m away. Distraction display may occur at any time during the breeding season, although it is usually most frequent and intense about the time of hatching. Both birds of a pair may simultaneously engage in distraction displays, especially in areas of high density of nests or broods, when as many as a dozen adults may converge on an intruder. In isolated pairs, one bird may take charge of leading the young to safety while the other displays toward the intruder.

NESTING

Nests.—Of 86 nests, 69 were on raised sandspits with little or no slope, the remainder on the lower slopes of dunes. Small stones (1–12 cm diameter) were scattered around 31 of 38 nests. Of these, "nearest object" (disregarding vegetation, which would be absent or tiny when nests were initiated) was <0.5 m from one nest and >6 m from 31 nests. In general, nests were not near vegetation on broad beaches but on narrow beaches (as little as 2 m wide) they were sometimes under tufts of marram grass. On extensive tracts of open beach habitat the birds had a wide field of view, and on average left their nests when intruders were 43.1 ± 21.2 m away ($N = 66$, range = 5–93 m). Choice of nest-site in Piping Plovers, in contrast to other Charadrii (Graul 1975), is not tied to proximity of vegetation or physiographic features.

Some Piping Plover nests are lined with fragments of sea shell, accumulated during courtship and incubation. Nests on sand or a sand-gravel surface are unlined, whereas nests on beaches strewn with broken shells are usually lined to some extent. A lining of bleached sea shells increases nest visibility from above, but probably does not aid adults in finding nests, since they normally approach the nest-site on foot. White shell linings are particularly conspicuous in wet weather when the sand color darkens. Three clutches disappeared (lost to predators) from lined nests during heavy rain.

Lining the nest is widespread among plovers. In Red-capped Dotterels the amount of nesting material depends on dampness of the site (Hobbs 1972). Improved drainage due to lining may not be critical to nesting success in Piping Plovers as three watersoaked clutches hatched successfully, suggesting considerable tolerance to moisture.

Egg-laying.—Established pairs court and copulate repeatedly before and during the egg-laying period. Scrapes appeared in territories up to 2 weeks before females selected scrapes and laid first eggs. Copulation and other associated displays fall off rapidly after the clutch is completed, although pair bonds are maintained.

In two cases clutches were completed in 6 days and in one case in 5 days. Intervals between successive eggs ranged from 44–54 h in seven instances, but two intervals were 72 h and 77 h each. These values agree with Wilcox (1959), who reported eggs laid on alternate days, with the clutch completed in 6 days.

Eggs.—The pale buff eggs are marked with fine splotches of black, brownish-black or purplish-black. Markings are usually distributed quite evenly, but some eggs have more, larger, and darker spotting at the broad end. Within clutches intensity and size of markings are usually quite similar.

For 215 eggs from 56 clutches, mean length was 32.5 ± 0.955 mm (range = 29.6–35.4) and mean breadth was 24.8 ± 0.5 mm (range = 23.4–26.1). The mean index of egg volume (length \times breadth²) was $19,927 \pm 1054.3$ mm³ (range = 16,486–22,387). A one-way analysis of variance performed on dimensions of the 16 eggs from six clutches whose order of laying in the clutch was known, showed no significant differences ($P \leq 0.05$) among the four clutch positions. However, highly significant differences ($P \leq 0.01$) in dimensions were found among the clutches of individual females.

Piping Plovers raise one brood per year. Mean clutch-size was 3.96 ± 0.2 ($N = 68$, range = 3–4). Clutches laid later in the breeding season are often smaller and Tufts (1973) suggested that Piping Plovers in Nova Scotia tend to lay fewer eggs in second clutches. The only three 3-egg clutches found were all first clutches.

Incubation.—During the daytime both sexes incubate, probably about equally. In 12.1 h of observations at two nests, females incubated 6.1 h and males 6.0 h. Nest relief involves elements of display and predator distraction. A bird involved in exchanging incubation duties with its mate announces its arrival with one or two notes. The sitting bird usually responds vocally and sometimes also tosses to either side shell fragments from the edge of the nest. The approaching bird always walks to the nest, occasionally shell-tossing. Preferred directions and routes for approaching and leaving are indicated by tracks. At the mate's approach the incubating bird walks from the nest; it too may shell-toss and preen briefly. When being relieved male birds sometimes move away in a low crouched walk similar to the low gliding run of courtship. The relieving bird settles immediately onto the eggs uttering soft throaty peeps. If the departing bird

leaves the territory one or two single peep notes or "peep-low" calls may be given. If the off-duty bird remains it usually squats on the sand some distance from the nest (often at regular sites) closely resembling an incubating bird. Mean time of daytime incubation bouts was 79.4 ± 47.3 min ($N = 17$, range = 25–153).

When untended nests are filled in with sand, adults use rapid shuffling foot movements to search for eggs, and kick sand away to uncover them. In contrast, Killdeer (Nickell 1943), and Little Ringed and Kentish plovers (Walters 1956) use the bill to locate and uncover buried eggs.

Hatching.—The incubation period (considered here to be time from laying of last egg until hatching of last egg) was 28 days for five clutches, 27 days in one clutch and 29 in another. Two clutches in nests 3 m apart took minimally 31 and 38 days to hatch, because of the greater than normal time devoted to territorial interaction between these adjacent pairs.

Protracted incubation periods for European Oystercatchers (*Haematopus ostralegus*) have been attributed to time adults were kept off the nest by human disturbance (Keighley and Buxton 1948). A case of prolonged incubation period in the Spotted Sandpiper (*Actitis macularia*) (Hays 1972) was attributed to a delay in initiation of steady incubation due to the too close proximity of another nest.

One mateless female Piping Plover incubated her four eggs for a minimum of 39 days before deserting. In contrast, Boyd (1972) and Rittinghaus (1956) reported that widowed female Snowy and Kentish plovers deserted within 4–6 days after the disappearance of a mate.

There was no indication within clutches that eggs laid earlier hatched sooner; most hatched within 4–8 h. However, in a few clutches the hatching period lasted up to 45 h, usually involving delay of only one egg. Eggs failing to hatch were abandoned within 1–2 days. Egg shells are carried on foot up to 40 m from the nest; one bird flew with the shell after walking 10 m.

In 1975, peak hatching occurred during the second and third weeks of June. Probably a number of late June and July hatchings are renests. My observations in 1977, 1978, and 1979 showed peak hatching periods during the third and fourth weeks of June on beaches in New Brunswick, Prince Edward Island, and the Magdalen Islands, where delayed nesting may be related to a longer migration route and the later spring in the Gulf of St. Lawrence. Latest known hatching occurred about 27 July 1977, at Cavendish, P.E.I. The one known nest of a first year bird, a male, contained eggs that hatched 6–8 July 1976.

Out of 25 nests checked on Cadden Beach in 1975, 77 young hatched from 97 eggs, a 79.4% hatching success. Average number of young hatch-

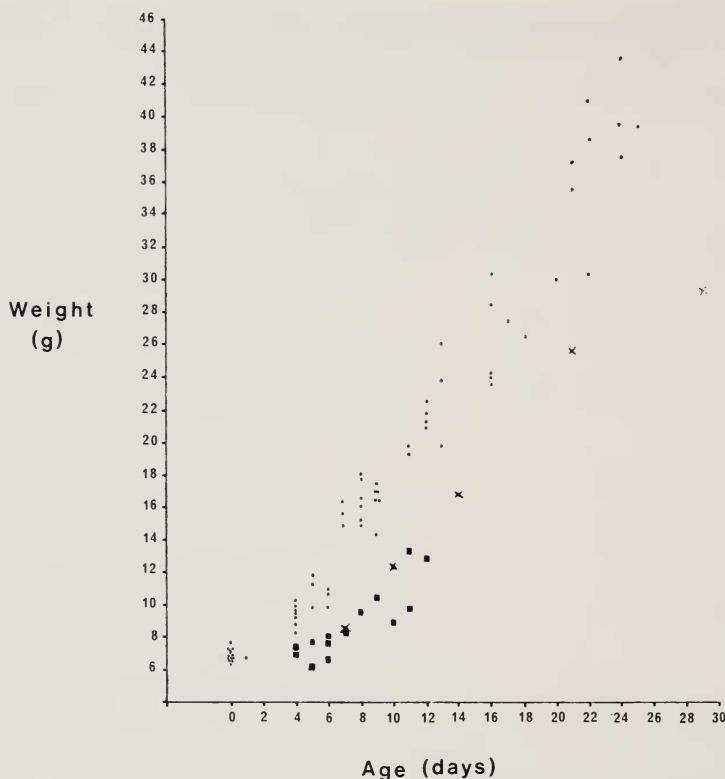


FIG. 4. Weight development of chicks. Dots denote chicks believed to have fledged, squares denote chicks dying before 14 days, and x's indicate values (sample size not reported) given by Wilcox (1959).

ing per nest was 3.08. In 1976, 104 eggs were found in 26 nests of which 75 hatched for a success rate of 72.1% or an average of 2.88 chicks hatched per nest. Of the 49 of 201 eggs which failed to hatch nine were damaged during handling or trapping; 17 were destroyed by mammals or birds (cattle, and probably gulls [*Larus*] or crows [*Corvus*]); and 23 were abandoned in the nest. Wilcox (1959) found somewhat higher success among Long Island Piping Plovers over a 20-year period: 91% hatching, an average of 3.52 young per nest.

Young.—Fig. 4 presents weight development of chicks. Chicks which fail to achieve about 60% of normal weight by day 12 are unlikely to survive. Wilcox (1959) reported chick weights somewhat lower than those obtained on Cadden Beach. Cadden Beach chicks having growth incre-

TABLE 1
PIPING PLOVERS FLOCKING WITH OTHER SPECIES PRIOR TO MIGRATION

	Piping Plovers	Other species (N)	Activity
11 July '75	3 adults	'peep' (112)	feeding
14 July '76	27 adults 7 juv.	Least Sandpiper (110)	feeding
15 July '76	12	Least Sandpiper (65)	flying, calling
22 July '76	16	Least Sandpiper (50)	flying, calling
	4	Least Sandpiper (4)	flying, calling
23 July '76	3 adults	Sanderling (3)	feeding
	1 juv.	Semipalmated Sandpiper (2)	
		Least Sandpiper (1)	

ments during their first 10 days as low as those reported by Wilcox (1959) without exception failed to survive.

Two chicks 25 days old could fly >15 m, while two others could fly <2 m. Young of two broods aged 28 and 32 days were flying well. These fledging times are somewhat shorter than the 30–35 days reported by Wilcox (1959).

Fledging success is difficult to assess since older chicks become increasingly elusive. I considered that a chick survived to fledging if when last caught it was known or estimated to be at least 10 days old and exhibited a normal growth pattern at the time (see Fig. 4). The fate of 75 chicks hatching from known nests has been assessed as follows: 29 presumed dead, 28 presumed fledged, and 18 unknown. In addition, at least 11 chicks from nests that were not found are believed to have fledged. Thus, between 39 and 57 chicks may have fledged from Cadden Beach in 1976. This represents approximately 1.3–2.1 chicks fledged per pair. On eight smaller, accessible, recreational beaches 15 pairs fledged between 11 and 17 young or 0.7–1.1 young fledged per pair.

Data on fledging success in other plover species are scarce. For the Ringed Plover fledging rates of one chick per pair (Laven 1940) and 1.28 chicks per pair (Prater 1974) have been reported. Boyd (1962) gave 1.55–2.22 young fledged per pair in Little Ringed Plover and Graul (1975) cited a ratio of one juvenile to three adults in pre-migration flocks of Mountain Plover.

Flocking and departure.—By early July some adults and the oldest of the fledged juveniles increasingly flock on neutral feeding areas and associate with other migrants such as Least Sandpiper (*Calidris minutilla*),

Greater Yellowlegs (*Tringa melanoleucus*), Sanderling (*Calidris alba*), Semipalmated Plover and Spotted Sandpiper (see Table I). Migrating Piping Plovers often give two-note calls while in flight.

SUMMARY

A population of approximately 27–29 pairs of Piping Plovers (*Charadrius melodus*) was studied in southern Nova Scotia in 1975 and 1976. Birds arrived in late April, occupied nesting and feeding territories, and initiated courtship. The aerial display flight of males is similar to that of several other plover species and is used to advertise territorial possession and attract prospective mates. Horizontal threat charges, and ground or aerial chases are used in the establishment of territorial boundaries. Parallel-run displays are more frequently used for boundary maintenance. Scraping, tilt display, and copulatory and distraction behaviors are generally similar to those of other *Charadrius* spp. Mean size of nesting territories was 4000 m² and nests averaged about 52 m apart. Of 68 clutches 65 had four eggs and three had three eggs. Most eggs were laid at approximately 48-h intervals; the longest interval was 77 h. Incubation averaged 28 days; one extreme of 38 days was recorded. Egg size varied significantly among females but not with order of laying. Average number of young hatching per nest was 3.08 in 1975 and 2.88 in 1976. Growth rates for most chicks were higher than those reported for birds in New York.

ACKNOWLEDGMENTS

The study was funded in part by a National Research Council of Canada grant to I. A. McLaren at Dalhousie University, where I was supported by a Killam Scholarship. Logistic support was provided by the Nova Scotia Department of Lands and Forests. Financial assistance was received from the Prince Edward Island Department of the Environment for the 1977 and 1978 work and from the Senate Research Committee of the University of P.E.I. in 1979. I thank H. Rueggeberg for assistance in the field, D. Cairns, and J. C. Barlow for critically reviewing the manuscript, and I. A. McLaren for advice and guidance throughout the study.

LITERATURE CITED

- BENT, A. C. 1929. Life histories of North American shore birds. Pt. 2. U.S. Natl. Mus. Bull. No. 146.
- BOYD, H. 1962. Mortality and fertility of European Charadrii. Ibis 104:368–387.
- BOYD, R. L. 1972. Breeding biology of the Snowy Plover at Cheyenne Bottoms Waterfowl Management Area, Barton County, Kansas. MSc. thesis, Kansas State Teachers College, Emporia, Kansas.
- BUB, H. 1962. Planberingungen am Sandregenpfeifer (*Charadrius hiaticula*). J. Orn. 103: 243–249.
- CAIRNS, W. E. AND I. A. McLAREN. 1980. Status of the Piping Plover on the east coast of North America. Am. Birds 34:206–208.
- EDWARDS, G., E. HOSKING, AND S. SMITH. 1947. Aggressive display in the Ringed Plover. Br. Birds 40:12–19.
- GLUTZ VON BLOTZHEIM, U. N., K. M. BAUER, AND E. BEZZEL. 1975. Handbuch der Vogel Mitteleuropas VI (1). Akademische Verlagsgesellschaft. Frankfurt am Main, Germany.
- GRAUL, W. D. 1973a. Possible functions of head and breast markings in Charadriinae. Wilson Bull. 85:60–70.

- . 1973b. Adaptive aspects of the Mountain Plover social system. *Living Bird* 12: 69–94.
- . 1975. Breeding biology of the Mountain Plover. *Wilson Bull.* 87:6–31.
- HALL, K. R. L. 1964. A study of the Blacksmith Plover *Hoplopterus armatus* in the Cape Town area. II. Behaviour. *Ostrich* 35:3–16.
- HAYS, H. 1972. Polyandry in the Spotted Sandpiper. *Living Bird* 11:43–57.
- HOBBS, J. N. 1972. Breeding of Red-capped Dotterel at Fletcher's Lake, Dareton, N.S.W. *Emu* 72:121–125.
- KEIGHLEY, J. AND E. J. M. BUXTON. 1948. The incubation period of the Oystercatcher. *Br. Birds* 61:261–266.
- LAVEN, H. 1940. Beitrage zur Biologie des Sandregenpfeifers (*Charadrius hiaticula* L.). *J. Orn.* 88:183–287.
- LENINGTON, S. AND T. MACE. 1975. Mate fidelity and nesting site tenacity in the Killdeer. *Auk* 92:149–151.
- MACLEAN, G. L. 1972. Problems of the display postures in the Charadrii (Aves: Charadriiformes). *Zool. Afric.* 7:57–74.
- MASON, A. G. 1947. Territory in the Ringed Plover. *Br. Birds* 40:12–19.
- NICKELL, W. P. 1943. Observations on the nesting of the Killdeer. *Wilson Bull.* 55:23–28.
- PHILLIPS, R. E. 1972. Sexual and agonistic behavior in the Killdeer (*Charadrius vociferus*). *Anim. Behav.* 20:1–9.
- PRATER, A. J. 1974. Breeding biology of the Ringed Plover *Charadrius hiaticula*. Pp. 15–22 in *Proc. IWBR Wader Symposium*, Warsaw, Poland.
- RITTINGHAUS, H. 1956. Untersuchungen am Sandregenpfeifer (*Charadrius alexandrinus* L.) auf der Insel Oldeog. *J. Orn.* 97:117–155.
- SIMMONS, K. E. L. 1953a. Some studies on the Little Ringed Plover. *Avic. Mag.* 59:191–207.
- . 1953b. Some aspects of the aggressive behaviour of three closely related plovers (*Charadrius*). *Ibis* 95:115–127.
- . 1956. Territory in the Little Ringed Plover *Charadrius dubius*. *Ibis* 98:390–397.
- SLUITERS, J. E. 1938. Bijdrage tot de biologie van den Kleinen Plevier (*Charadrius dubius curonicus* Gm.). *Ardea* 27:123–151.
- SPENCER, K. G. 1953. *The Lapwing in Britain*. A. Brown and Sons, London, England.
- SUTTON, G. M. AND D. F. PARMELEE. 1955. Breeding of the Semi-palmated Plover on Baffin Island. *Bird-Banding* 26:137–147.
- TOMKINS, I. R. 1944. Wilson's Plover in its summer home. *Auk* 61:259–269.
- TUFTS, R. W. 1973. *The birds of Nova Scotia*. Nova Scotia Museum, Halifax, Nova Scotia.
- WALTERS, J. 1956. Eiruckgewinnung und Nistplatzorientierung bei See- und Flussregenpfeifer (*Charadrius alexandrinus* und *dubius*). *Limosa* 29:103–129.
- WILCOX, L. 1939. Notes on the life history of the Piping Plover. *Birds of Long Island*, No. 1:3–13. Bird Club of Long Island, Long Island, New York.
- . 1959. A twenty year banding study of the Piping Plover. *Auk* 76:129–152.
- WITHERBY, H. F., F. R. C. JOURDAIN, N. P. TICEHURST, AND B. W. TUCKER. 1965. *The handbook of British Birds*. Vol. IV. London, England.

BIOLOGY DEPT., DALHOUSIE UNIV., HALIFAX, NOVA SCOTIA B3H 4J1, CANADA. (PRESENT ADDRESS: 60 NEWLAND CRES., CHARLOTTETOWN, PRINCE EDWARD ISLAND C1A 4H7, CANADA.) ACCEPTED 22 APR. 1982.